

STIMULUS CONTROL AND RESPONSE BIAS IN AN ANALOGUE PREY-DETECTION PROCEDURE

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The present study compared the performance of 6 pigeons trained to detect luminance differences in two different signal-detection procedures. Exposed to a three-key array, the pigeons were trained to peck the left key when the brighter of two light intensities had been presented on the center key and to peck the right key when the dimmer of two light intensities had been presented on the center key. Procedure A was a standard signal-detection procedure in which left/bright and right/dim responses produced food reinforcement and left/dim and right/bright responses produced periods of timeout. Procedure B was designed to simulate some of the contingencies operating in a prey-detection situation. Left-key responses produced reinforcement following the brighter center-key stimulus and a period of timeout following the dimmer center-key stimulus. Right-key responses always produced a short period of timeout irrespective of the stimulus. Within each procedure, the duration of timeout arranged for false alarms (left/dim responses) was varied between 3 s and 120 s. Measures of accuracy and response bias were compared between the two procedures. The timeout manipulation produced systematic, but relatively small, changes in these measures when right/dim responses (i.e., correct rejections) produced reinforcement (Procedure A). Arranging timeout for right/dim responses in Procedure B produced greater variability in accuracy and response bias than did arranging reinforcement, but this variability was not related to timeout duration. Overall, discrimination accuracy was considerably higher when right/dim responses produced timeout than when they resulted in reinforcement, and accuracy was accompanied by a large bias toward the response associated with reinforcement. These results are consistent with a recently proposed model of signal detection.

Key words: signal detection, stimulus control, response bias, prey detection, key peck, pigeons

A predator searching for cryptic prey is faced with a situation in which prey transmit sensory cues that cannot be discriminated with certainty from cues provided by nonprey (Curio, 1976; Edmunds, 1974; Endler, 1981, 1986). The decision to attack or reject a potential prey item must be made on the basis of this imperfect sensory information. This task is directly analogous to the requirements of the yes-no paradigm in signal-detection theory (e.g., Green & Swets, 1966/1974).

In a laboratory analogue of this situation, subjects are trained to emit one of two responses (left- or right-key pecks) following the presentation of one of two stimuli (bright or dim center keylights). Figure 1 shows the four events defined by the possible combinations of the stimulus and response classes. Hits (left/bright) and correct rejections (right/dim) are usually reinforced, whereas misses (right/

bright) and false alarms (left/dim) either have no scheduled consequence or are punished. Thus, the standard detection matrix is diagonally symmetrical, in the sense that hits and correct rejections have a common outcome, as do misses and false alarms.

The possible outcomes of an encounter between a predator and a potential prey item can also be represented in a stimulus-response matrix. In this case, the two stimuli are prey and nonprey and the responses are attack or reject. Each stimulus-response event is associated with some "fitness" cost or benefit to the predator (Staddon, 1983). Attacking a prey item (a hit) obviously contributes some benefit, whereas rejecting a prey item (a miss) or attacking a nonprey item (a false alarm) produce some cost to the predator, the magnitude of which may depend on a number of factors. Staddon suggested that correctly rejecting a nonprey item (a correct rejection) has no fitness consequence.

In a series of experiments, Kamil and his associates have simulated the interaction between an avian predator, the blue jay (*Cyanocitta cristata*), and the cryptic Catocala moth (*Noctuidae*) using signal-detection procedures. On each trial, blue jays were presented with a slide, which may or may not contain a moth,

We thank the Auckland University Research Committee for their support of this research. In addition, we are indebted to the staff and students who helped conduct the experiment and to Jacqui Barrett for her careful supervision of all aspects of the animals' welfare. Correspondence and requests for reprints may be sent to Dianne McCarthy, Department of Psychology, University of Auckland, Private Bag 92019, Auckland, New Zealand.

		Responses	
		Left	Right
Stimuli	Bright	HIT	MISS
	S ₁	RFT	EXT
	Dim	FA	CR
	S ₂	EXT	RFT

Fig. 1. The matrix of stimulus and response events in the animal analogue of the yes-no procedure. RFT and EXT denote reinforcement and extinction, respectively. A left/bright response is called a hit (H), a right/bright response is called a miss (M), a left/dim response is called a false alarm (FA), and a right/dim response is called a correct rejection (CR).

and could either attack or reject that slide by pecking one of two response keys. Pietrewicz and Kamil (1977) demonstrated that the type of substrate on which the moth is resting, the bird's orientation, and its distance from the moth all affected the accuracy of prey detection. Other studies have investigated the search-image hypothesis (Pietrewicz & Kamil, 1979, 1981), the effects of the time between slide presentations (travel time) on the accuracy and latency of responding (Getty, Kamil, & Real, 1987; Kamil, Lindstrom, & Peters, 1985; Kamil, Peters, & Lindstrom, 1982), and the effects of depletion on patch choice when prey are conspicuous (Kamil & Yoerg, 1985; Kamil, Yoerg, & Clements, 1988). These studies have employed two distinct forms of stimulus-response matrix. The first is depicted in Figure 2. This matrix differs from the standard yes-no matrix (Figure 1) in that although attacking a moth slide (hit) produces reinforcement, rejecting a no-moth slide (correct rejection) does not. These outcomes are consistent with the "natural" contingencies outlined by Staddon (1983). However, two features of this matrix are potentially at odds with natural contingencies.

First, attacking a no-moth slide (false alarm) and rejecting a moth slide (miss) were punished with equal durations of timeout from reinforcement. However, in a natural situa-

tion, the two types of error could have very different consequences. Rejecting available prey will clearly lower the local, or even the overall, rate of energy intake, the consequences of which will vary according to the type of predator and its metabolic requirements. Similarly, depending on the type encountered, attacking nonprey items may incur a great variety of costs. A predator may simply expend the time and energy involved in handling and then rejecting the item, or the consequences may be much more severe. Second, different consequences were arranged for the two types of prey rejections, providing feedback on the accuracy of decisions to reject a potential prey item. Such feedback is not usually provided in the natural situation. This last criticism does not apply to the second type of matrix employed by Kamil (Figure 3), because all prey-rejection responses produced the same outcome.

The present study was designed to compare the performance of pigeons trained to detect luminance differences in two different signal-detection procedures. One procedure (A) employed the standard yes-no matrix (Figure 4) in which correct rejections produced reinforcement, whereas the contingencies arranged in the other procedure (B; Figure 5) were designed to correspond more closely with natural prey-detection contingencies, with correct re-

		Responses	
		Attack	Reject
Stimuli	Moth	H RFT	M 30 s
	No moth	FA 30 s	CR ---

Fig. 2. The matrix of stimulus and response events used by Pietrewicz and Kamil (1981, Experiment 1). Attack was defined as the completion of eight responses on the stimulus key, and reject as a single response on an advance key. An additional 3-s intertrial interval followed all consequences.

		Responses	
		Attack	Reject
Stimuli	Moth	H RFT + 3 s	M ---
	No moth	FA ---	CR ---

Fig. 3. The matrix of stimulus and response events used by Getty et al. (1987) and Kamil et al. (1985, 1988). Attack was defined as the completion of a fixed-interval 30-s schedule on the stimulus key, and reject as a single response on an advance key. A 2-s intertrial interval followed all consequences.

		Responses	
		Left	Right
Stimuli	Bright S_1	H 3-s RFT	M 3-s TO
	Dim S_2	FA v-s TO	CR 3-s RFT

Fig. 4. The matrix of stimulus and response events in Procedure A. S_1 (bright) and S_2 (dim) are the two light intensities used as sample stimuli. Pecks to the left and right side keys are the two responses. RFT, EXT, and TO denote reinforcement, extinction, and timeout, respectively.

jections producing timeout. Previous research (e.g., Kamil *et al.*, 1985) has demonstrated that the prey-detection matrix (Figure 3) represents a stable detection situation. In the present experiment, left- and right-key responses in the choice phase were analogous to attacking and rejecting prey (bright center-key stimulus) and nonprey (dim center-key stimulus), respectively. Side-key responses produced either reinforcement or a period of timeout from reinforcement (Ferster & Skinner, 1957; Leitenberg, 1965). As is conventional in research with pigeons, timeout was equated with blackout (i.e., all chamber lights turned off). The duration of timeout arranged for false alarms was varied parametrically in both procedures. In ecological terms, this manipulation is analogous to varying the cost of incorrectly attacking a nonprey item. Measures of the degree to which the center-key stimuli controlled responding (i.e., discrimination accuracy) and measures of the extent to which side-key preference was affected by the different contingencies (i.e., response bias) were compared between the two procedures. Two key questions were asked: (a) Would measures of stimulus control remain unaffected when stimulus vari-

ables assumed to be unrelated to the stimuli (such as reinforcement and timeout) were manipulated? (b) Would the different contingencies produce different degrees of response bias?

Three measures of stimulus control were compared—proportion correct, A' (Grier, 1971), and $\log d$ (Davison & Tustin, 1978)—and were computed using the following equations:

Proportion correct

$$= (H + CR) / (H + M + FA + CR), \quad (1)$$

$$A' = 0.5 + (H - FA) / (1 + H - FA)$$

$$\div (4 \cdot H \cdot [1 - FA]), \quad (2)$$

and

$$\log d = 0.5 \cdot \log(H \cdot CR / [M \cdot FA]). \quad (3)$$

In these equations, consistent with standard signal-detection terminology, H denotes hit (left/bright, Figures 4 and 5), M denotes miss (right/bright, Figures 4 and 5), FA denotes false alarm (left/dim, Figures 4 and 5), and CR denotes correct rejection (right/dim, Figures 4 and 5).

Two measures of response bias (or the de-

		Responses	
		Left	Right
Stimuli	Bright S_1	H 3-s RFT	M 3-s TO
	Dim S_2	FA v-s TO	CR 3-s TO

Fig. 5. The matrix of stimulus and response events in Procedure B. S_1 (bright) and S_2 (dim) are the two light intensities used as sample stimuli. Pecks to the left and right side keys are the two responses. RFT, EXT, and TO denote reinforcement, extinction, and timeout, respectively.

gree to which the animals favored responding on one alternative over the other) were compared— B'' (Grier, 1971) and $\log B$ (Davison & Tustin, 1978)—and were computed as follows:

$$B'' = (H[1 - H] - FA[1 - FA]) \div (H[1 - H] + FA[1 - FA]) \quad (4)$$

and

$$\log B = 0.5 \cdot \log(H \cdot FA / [M \cdot CR]). \quad (5)$$

METHOD

Subjects

Six experimentally naive homing pigeons, numbered 61 to 66, were maintained at $85\% \pm 15$ g of their free-feeding body weights by post session feeding of mixed grain. Water and grit were available at all times in the home cages.

Apparatus

A standard light-proof and sound-attenuating experimental chamber was used. The chamber contained three response keys, 20 mm in diameter, 90 mm apart, and 250 mm above

the grid floor. When operative, the center key could be transilluminated with various intensities of white light, and the two side keys could be transilluminated red. To be recorded, pecks to each key had to exceed approximately 0.1 N. Each effective response produced a brief feedback click. Responses on darkened keys had no scheduled consequences. A food magazine was situated 150 mm below the center key. During reinforcement, the keylights were extinguished, and the food magazine, which was filled with wheat, was raised and illuminated for 3 s. A houselight situated 55 mm above the center key provided the only other illumination in the chamber. The chamber was fitted with an exhaust fan that provided ventilation and helped to mask any external noise. All experimental events were controlled by a computer (a PDP® 8/e operating SUPERSKED® software for the first eight conditions and a PDP® 11/73 operating SKED-11® software for the remaining conditions) situated in an adjacent room.

Procedure

Initial training. The subjects were trained to eat from the food magazine and then, via shap-

Table 1

The sequence of experimental parts and conditions, the duration of timeout arranged for False Alarms (left/dim responses) in seconds, and the number of training sessions given in each condition. An "R" denotes that the condition was a replication of a previous condition.

Con- dition	Part	Procedure	Timeout duration	Sessions
1	1	A	3	16
2			10	25
3			20	18
4		B	20	42
5			10	30
6			5	34
7		A	20 (R)	14
8			3 (R)	37
9			3	40
10	2	B	3	35
11			20	34
12			5	28
13		A	10	27
14			20 (R)	31
15			20	33
16		B	5	30
17			10	27
18			60	34
19		A	30	29
20			120	35
21			120	24
22		B	30	21
23			60	26
24			60 (R)	30
25		A	3 (R)	28

ing, to peck all three keys using an autoshaping procedure (cf. Brown & Jenkins, 1968). Over 12 sessions, the key on which responses were reinforced and the key color (red, green, and white) were varied. The subjects then received four training sessions on a single variable-interval 7.5-s schedule, again with the key and key color varied across sessions.

Following this, the subjects received preliminary training on a discrete-trials luminance discrimination task. The birds were exposed to a three-key array. Initially, the two side keys were darkened, and one of two stimuli was presented on the center key. The center-key stimuli were two easily discriminable light intensities, and occurred with equal probability. The animals were trained to peck the left key when the brighter stimulus had been presented and to peck the right key when the dimmer stimulus had been presented by following these responses intermittently with 3-s access to wheat. Initially, the training was carried out using a correction procedure. That is, follow-

ing a left/dim or right/bright response, the center-key stimulus was re-presented on subsequent trials until the appropriate response was emitted. Following the appropriate response, each stimulus was equally likely to be presented on the next trial. Reinforcers for left/bright and right/dim responses were scheduled independently. That is, when the schedule on one key had set up a reinforcer, the schedule associated with the other key continued timing. It was possible, therefore, that both keys could have a reinforcer available at any one time. This is an uncontrolled reinforcer-ratio procedure (McCarthy, 1983; McCarthy & Davison, 1984), one that allows the distribution of responses between the alternatives to covary with the distribution of reinforcers. The probability of left-key and right-key reinforcers was .5 for nine sessions. The correction procedure was then discontinued, and reinforcers were arranged nonindependently (cf. Stubbs & Pliskoff, 1969). That is, when a left-key reinforcer, say, was arranged, it remained set up until a left/bright response was emitted. No reinforcers were available for right/dim responses until the left-key reinforcer was taken. This dependent-scheduling procedure (or controlled reinforcer-ratio procedure, McCarthy, 1983; McCarthy & Davison, 1984) ensures that the animal obtains the same distribution of reinforcers between the two keys as that arranged. The probability of reinforcement for left/bright responses was .8 for seven sessions and .2 for a further seven sessions in order to expose the animals to different distributions of reinforcers. Finally, reinforcers were again arranged independently with the probability of reinforcement for left/bright responses equal to .5. Stimulus disparity was systematically decreased over several sessions in order to select the stimulus pair for the first set of experimental conditions.

Experimental conditions. The sequence of experimental parts and conditions, and the number of training sessions given in each, are shown in Table 1. In all conditions, a trial commenced with one of two light intensities presented on the center key. The two side keys were initially darkened. For the first set of conditions (Part 1, Conditions 1 to 8), the luminance of the white center-key light was either 2.88 cd/m² (S₁) or 1.31 cd/m² (S₂). For the second set of conditions (Part 2, Conditions 10 to 25), S₁ remained unchanged, but S₂ was

1.97 cd/m². Thus, in Part 1, the luminance difference was 1.57 cd/m² and in Part 2, this difference was reduced to 0.91 cd/m². In all conditions of the experiment, S_1 was always the brighter of the two luminances and S_2 the dimmer; therefore, S_1 is hereafter referred to as "bright" and S_2 as "dim." The S_2 stimulus used in Condition 9 was of an intermediate, but unmeasured, intensity. A noncorrection procedure was employed in all conditions, and each stimulus was equally likely to be presented on any given trial.

One center-key response extinguished the center key and illuminated the two side keys red. In the conditions comprising Procedure A (Conditions 1 to 3, 8 to 10, 15 to 20, and 24 to 25), both left/bright and right/dim responses produced 3-s reinforcement (Figure 4), whereas in the conditions comprising Procedure B (Conditions 4 to 7, 11 to 14, and 21 to 23), left/bright responses produced 3-s reinforcement and right/dim responses produced a 3-s period of timeout (Figure 5). Thus, in all conditions, left/bright responses (hits) always produced 3-s reinforcement; right/dim responses (correct rejections) produced 3-s reinforcement in Procedure A and 3-s timeout in Procedure B. In all conditions, right/bright responses (misses) always produced a 3-s period of timeout, and left/dim responses (false alarms) produced a period of timeout, the duration of which varied within the range 3 s to 120 s across conditions within each procedure (see Table 1). During periods of timeout, all chamber lights were extinguished, and responses were ineffective and not recorded. A new trial began immediately after either the delivery of a reinforcer or a period of timeout.

Experimental sessions were conducted 7 days per week. Sessions began and ended in blackout after either 45 min or following the delivery of 40 reinforcers, whichever event occurred first. The data collected following each session were the number of left-key and right-key responses on S_1 (bright) and S_2 (dim) trials and the number of left-key and right-key reinforcers.

Experimental conditions were changed only when all subjects had satisfied the following stability requirement five, not necessarily consecutive, times. The median proportion of left-key responses calculated over the last five sessions did not differ from the median over the previous five sessions by more than .05. Thus,

a minimum of 14 sessions per condition was required to reach stability. Typically, once a subject had reached its individual criterion, it continued to show stable performance. On average, conditions were in effect for 29 sessions.

RESULTS

The Appendix shows the number of left- and right-key responses emitted by each subject on S_1 and S_2 trials. These data were summed over the final seven sessions of each condition. Note that the number of reinforcers delivered on the left and right keys in Procedure A equals the number of left/bright and right/dim responses emitted, and, in Procedure B, the number of reinforcers delivered on the left key equals the number of left/bright responses emitted. Measures of discrimination accuracy and measures of the control exerted by the various contingencies (i.e., response bias) were computed for each condition using the data shown in the Appendix. Additionally, and where appropriate, the ratio of reinforcers obtained from the left and right keys was computed for each condition in Procedure A. Of course, these ratios could not be computed for Procedure B, because no right-key reinforcers were scheduled in this set of conditions. All measures are shown first for Part 1, in which the luminance difference was 1.57 cd/m², and second for Part 2, in which the luminance difference was reduced to 0.91 cd/m².

Part 1: Stimulus Control

The degree to which the light intensities exerted control over the behavior of the animals was measured in three ways: proportion correct (Equation 1), A' (Equation 2), and log d (Equation 3). Note that, due to their log ratio nature, Equations 3 and 5 are indeterminate when one (or more) of the cell entries equals zero. For the individual-subject data, no right/bright responses (miss) were emitted in 21 of the 66 Procedure B conditions. To compute estimates of log d and log B for these conditions, a nonzero value (M') was substituted for M . To ensure that as little bias as possible be introduced, the following procedure was used: M' was taken to be the minimum of the number of S_1 trials multiplied by the overall proportion of errors (i.e., $FA/[H + FA + CR]$) and 1. In all cases, this procedure resulted in an M' value of 1, allowing

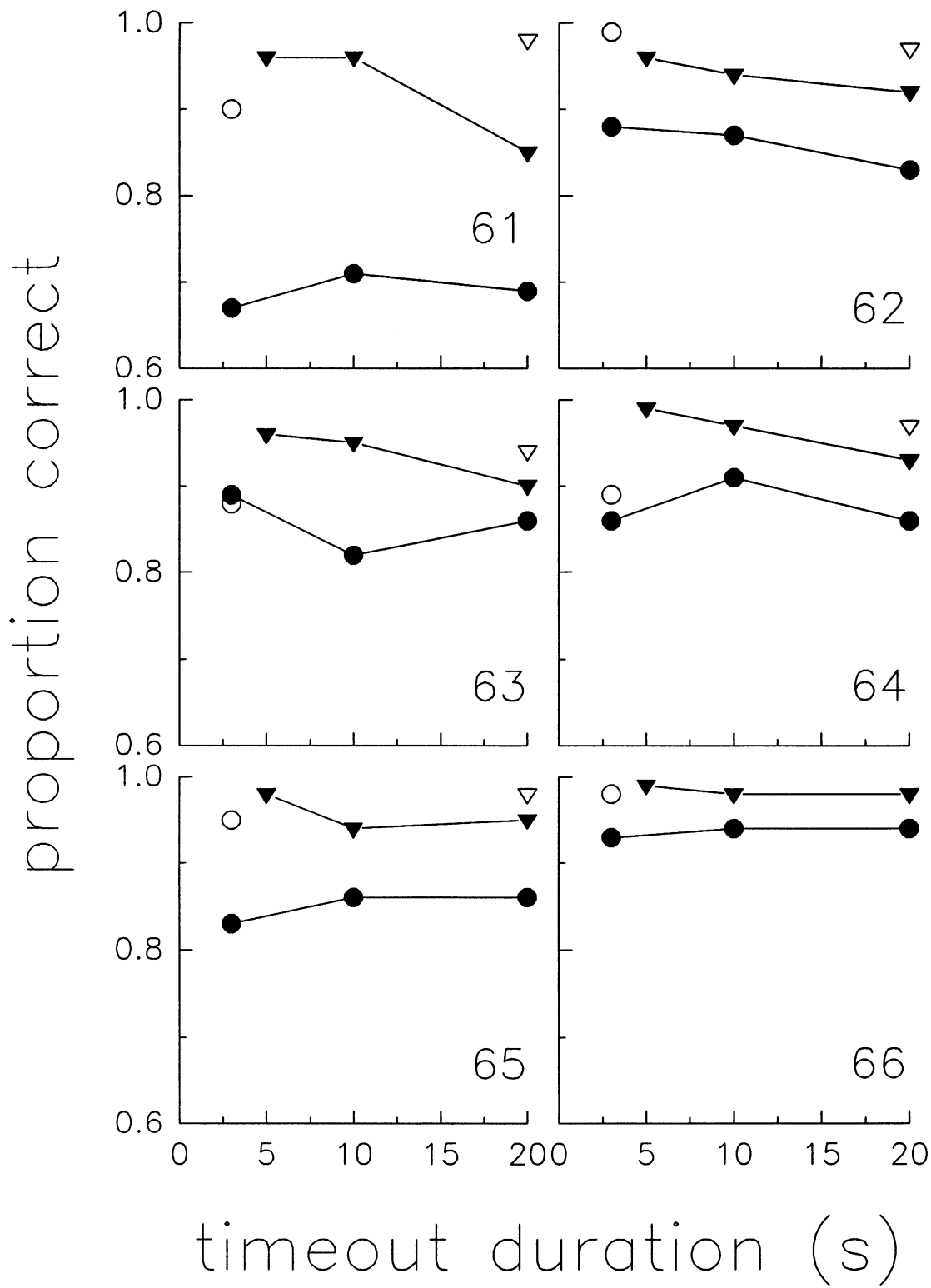


Fig. 6. Discrimination accuracy (as measured by proportion correct) as a function of the duration of blackout arranged for false alarms in the Procedure A (circles) and Procedure B (triangles) conditions of Part 1. Unfilled symbols represent replications.

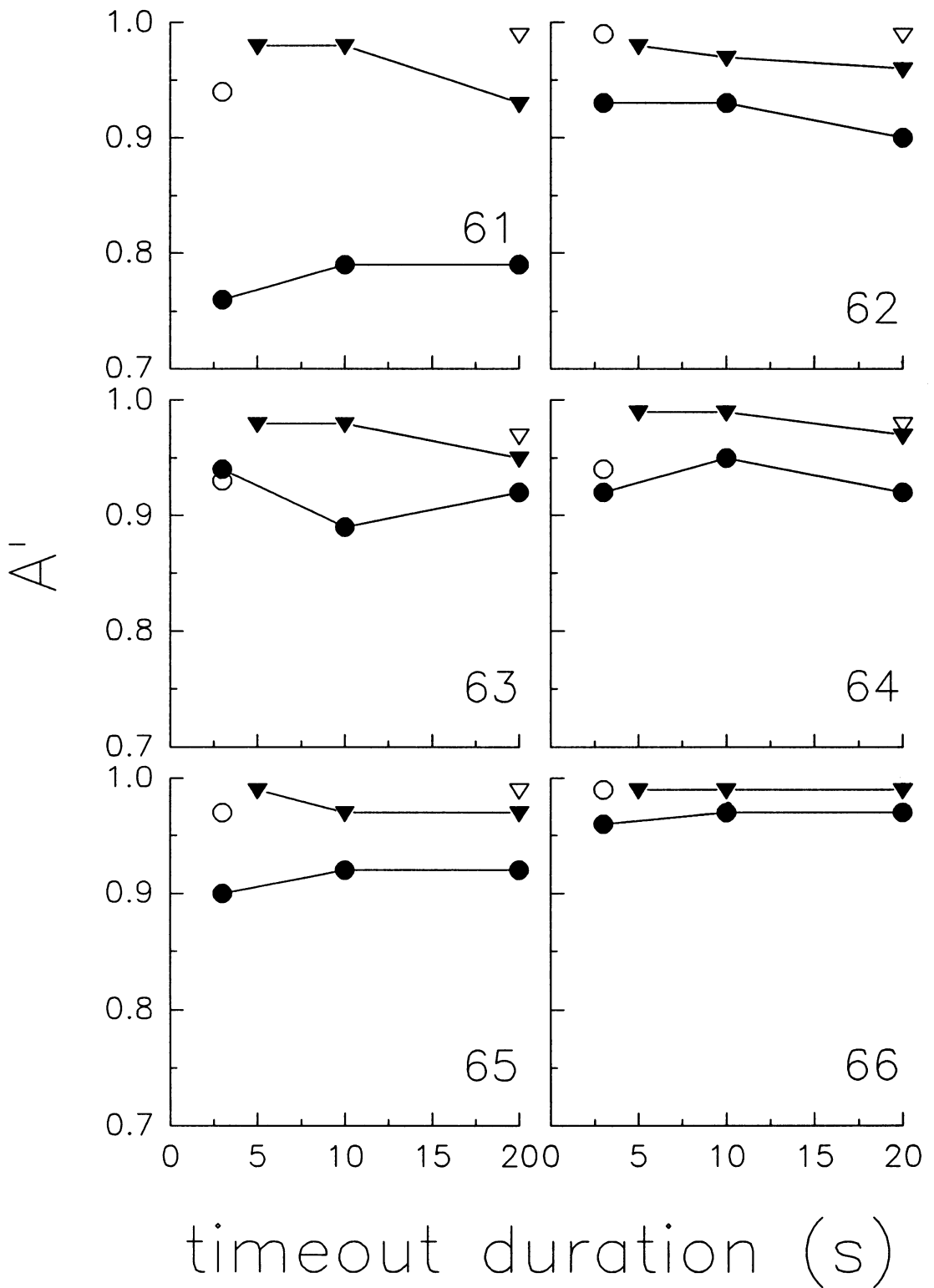


Fig. 7. Discrimination accuracy (as measured by A' ; Grier, 1971) as a function of the duration of blackout arranged for false alarms in the Procedure A (circles) and Procedure B (triangles) conditions of Part 1. Unfilled symbols represent replications.

noninfinite lower bounds to be determined for $\log d$ and $\log B$.

Figures 6, 7, and 8 show proportion correct, A' , and $\log d$, respectively, as a function of the duration of timeout arranged for false alarms (left/dim responses, Figures 4 and 5) for the Procedure A (circles) and Procedure B (triangles) conditions of Part 1. These measures are plotted separately for each subject. The most striking feature of these data was that for all subjects, these measures were higher when 3-s timeout (Procedure B) rather than 3-s reinforcement (Procedure A) was arranged for correct rejections (i.e., right/dim responses). Possible monotonic trends on these measures as a function of the duration of timeout for false alarms were assessed across subjects by nonparametric trend tests (Kendall, 1970). In all cases, the trends were nondirectional, and data points were averaged across replications. Although monotonic trends were evident for some birds, none of the three measures changed systematically across all subjects with increasing timeout duration in either procedure ($z = 2.34, p > .01$ in all cases). There was, however, some evidence of hysteresis in both procedures. In the replication of the Procedure A 3-s timeout condition (Condition 8), $\log d$ measures, for example, were in the same range as the Procedure B values for Birds 62 and 66 and took intermediate values for Birds 61 and 65. Because the timeout durations were presented in a decreasing order in Procedure B, some of the decreases in accuracy seen with increasing timeout duration may simply represent continued adjustment to the Procedure B contingencies. This conclusion is supported by the fact that accuracy measures for the replication of the Procedure B 20-s timeout condition (Condition 7) were generally higher than the original determinations.

Part 1: Contingency Control

Two measures of response bias were computed. Figures 9 and 10 show, respectively, B'' (Equation 4) and $\log B$ (Equation 5) as functions of the duration of timeout arranged for false alarms (left/dim responses, Figures 4 and 5) for the Procedure A (circles) and Procedure B (triangles) conditions of Part 1. These measures are plotted separately for each subject. Note that negative B'' values and positive $\log B$ values denote a bias toward responding on the left key, and positive B'' and negative \log

B values denote a bias toward responding on the right key.

Once again, performance was very different between the two procedures. Both measures showed that when 3-s reinforcement was arranged for correct rejections (right/dim responses; Procedure A), no significant biases were evident. However, when only one key (the left) produced 3-s reinforcement and 3-s timeout was arranged for right/dim responses (Procedure B), response bias was consistently large and toward the left key for both measures. Across subjects, there were no systematic changes in either measure in both procedures ($z = 2.34, p > .01$ for both measures in Procedure A, and $z = 1.92$ and 1.06 , respectively, for $\log B$ and B'' in Procedure B). However, monotonically increasing trends were evident on both measures for Birds 61, 62, and 63 in Procedure A and for Birds 64 and 66 ($\log B$) and Bird 66 (B'') in Procedure B.

In Procedure A, each subject's response bias (as measured by both B'' and $\log B$) changed with the obtained ratio of left/right reinforcers. The covariation of these measures was expected, given that an uncontrolled reinforcer-ratio procedure was used (Davison & McCarthy, 1988; McCarthy & Davison, 1984).

Summary

The major result of Part 1 was that very different measures of stimulus control and contingency control were obtained under Procedure A and B conditions. Specifically, measures of discrimination accuracy were higher, and response biases were more extreme, when 3-s timeout (Procedure B) rather than 3-s reinforcement (Procedure A) was arranged on the right key following presentations of the dimmer stimulus on the center key (correct rejections).

As a result of the (unexpectedly) high accuracy levels shown under timeout conditions in Procedure B by all subjects, Part 2 set out to vary timeout duration over a much wider range than in Part 1 while employing stimuli that were less easily discriminable.

Part 2: Stimulus Control

Figures 11, 12, and 13 show proportion correct, A' , and $\log d$, respectively, as a function of the duration of timeout arranged for false alarms (left/dim responses, Figures 4 and 5)

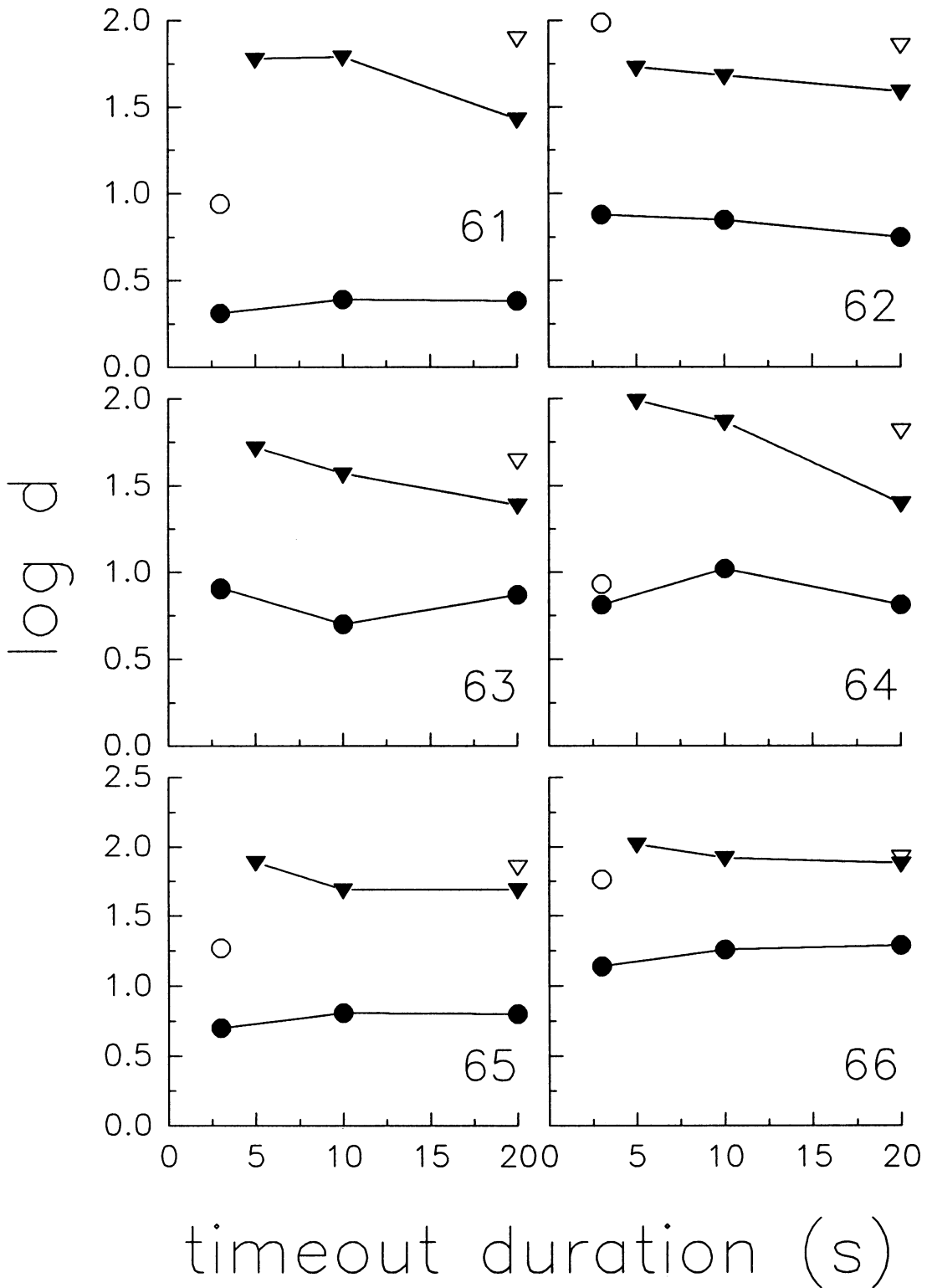


Fig. 8. Discrimination accuracy (as measured by $\log d$; Davison & Tustin, 1978) as a function of the duration of blackout arranged for false alarms in the Procedure A (circles) and Procedure B (triangles) conditions of Part 1. Unfilled symbols represent replications.

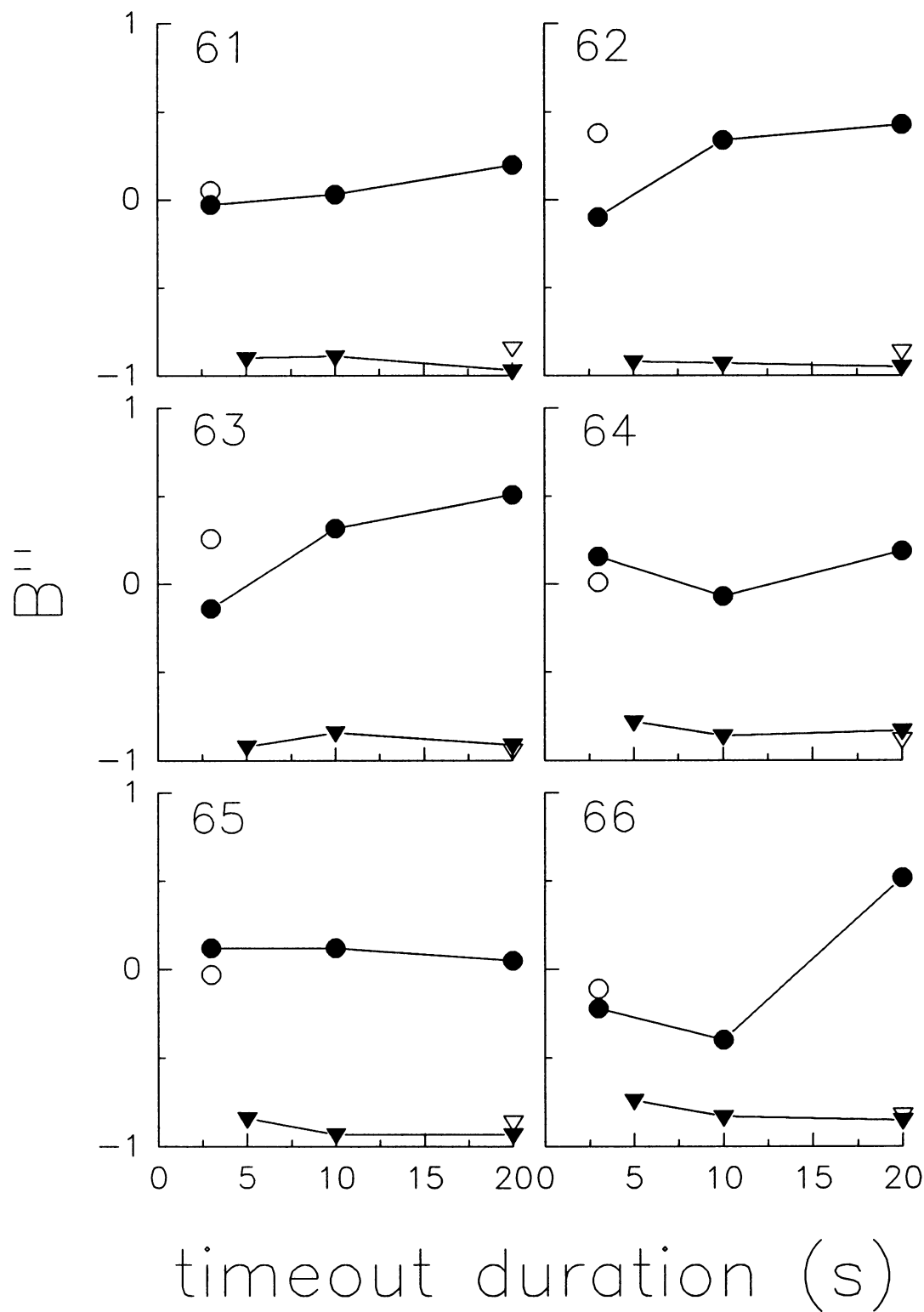


Fig. 9. Response bias (as measured by B' ; Grier, 1971) as a function of the duration of blackout arranged for false alarms in the Procedure A (circles) and Procedure B (triangles) conditions of Part 1. Unfilled symbols represent replications.

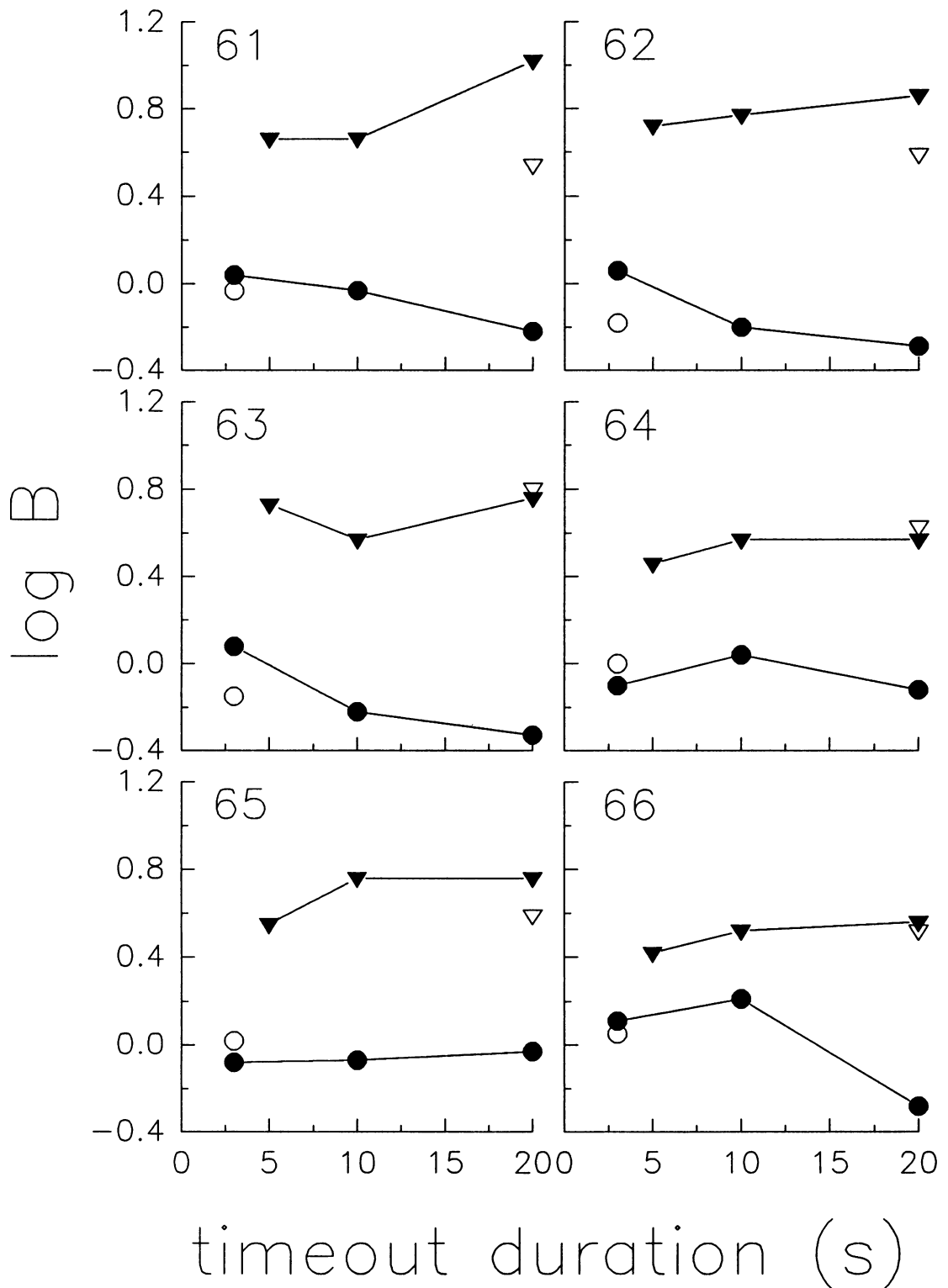


Fig. 10. Response bias (as measured by $\log B$; Davison & Tustin, 1978) as a function of the duration of blackout arranged for false alarms in the Procedure A (circles) and Procedure B (triangles) conditions of Part 1. Unfilled symbols represent replications.

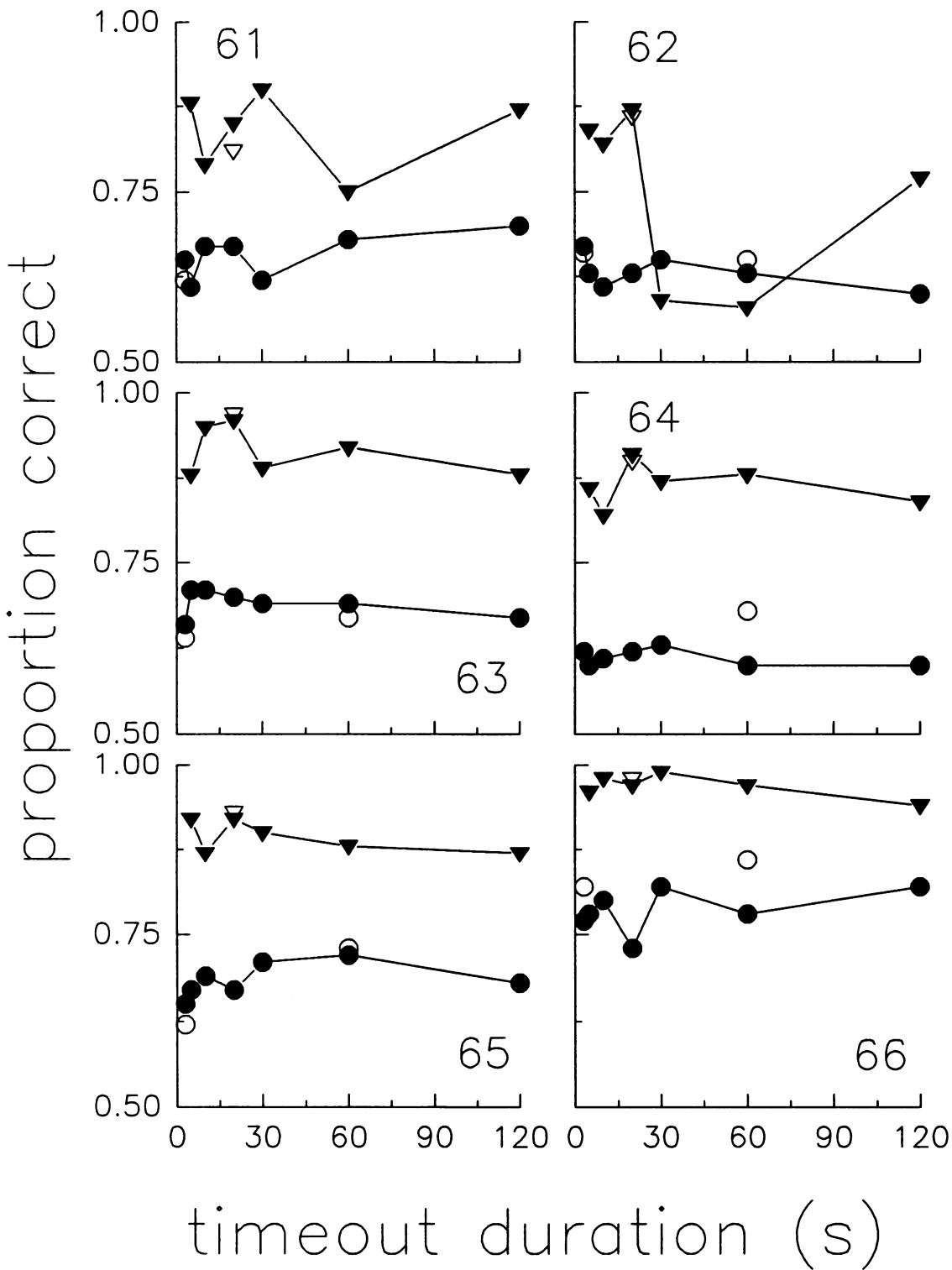


Fig. 11. Discrimination accuracy (as measured by proportion correct) as a function of the duration of blackout arranged for false alarms in the Procedure A (circles) and Procedure B (triangles) conditions of Part 2. Unfilled symbols represent replications.

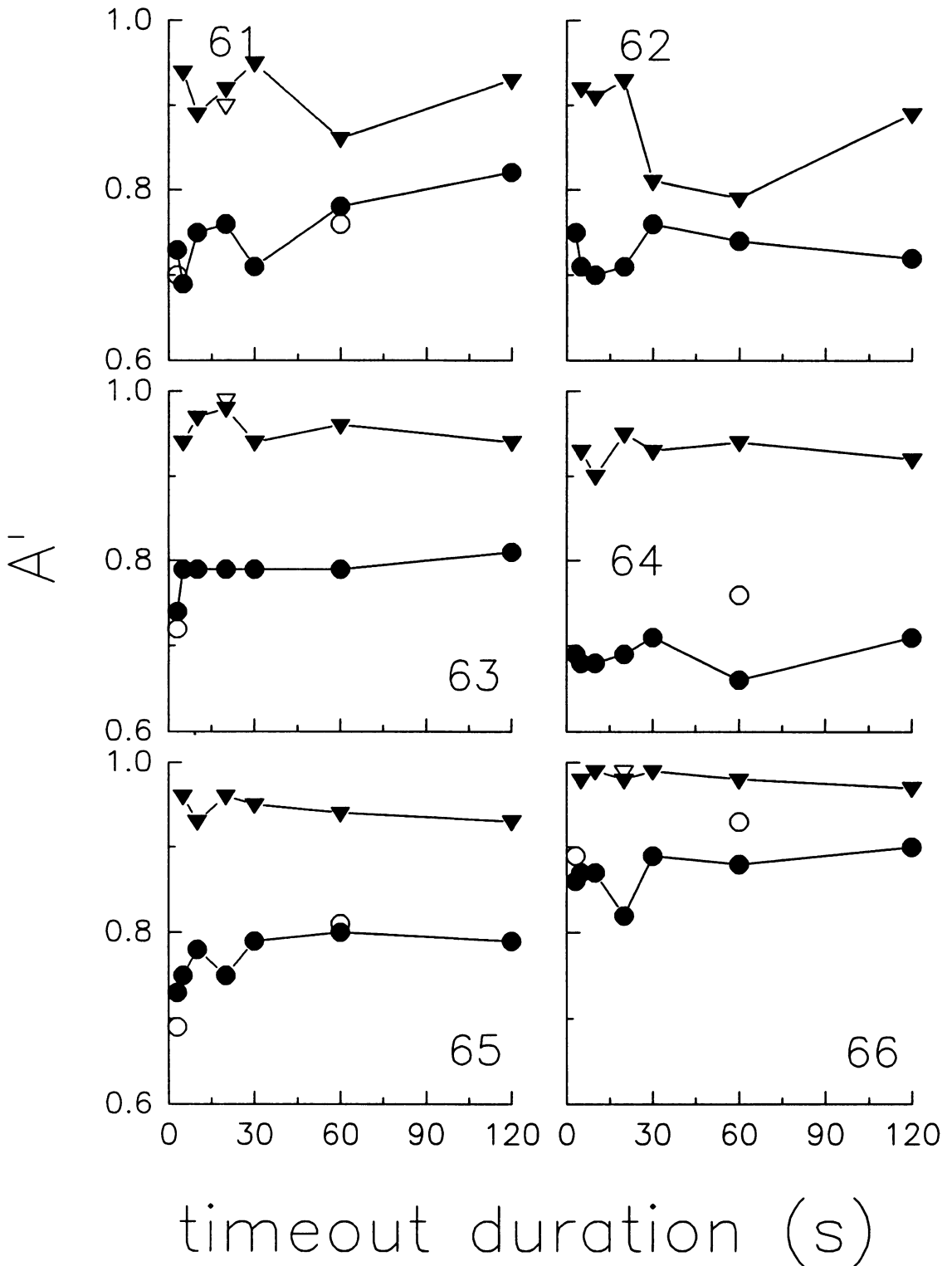


Fig. 12. Discrimination accuracy (as measured by A' ; Grier, 1971) as a function of the duration of blackout arranged for false alarms in the Procedure A (circles) and Procedure B (triangles) conditions of Part 2. Unfilled symbols represent replications.

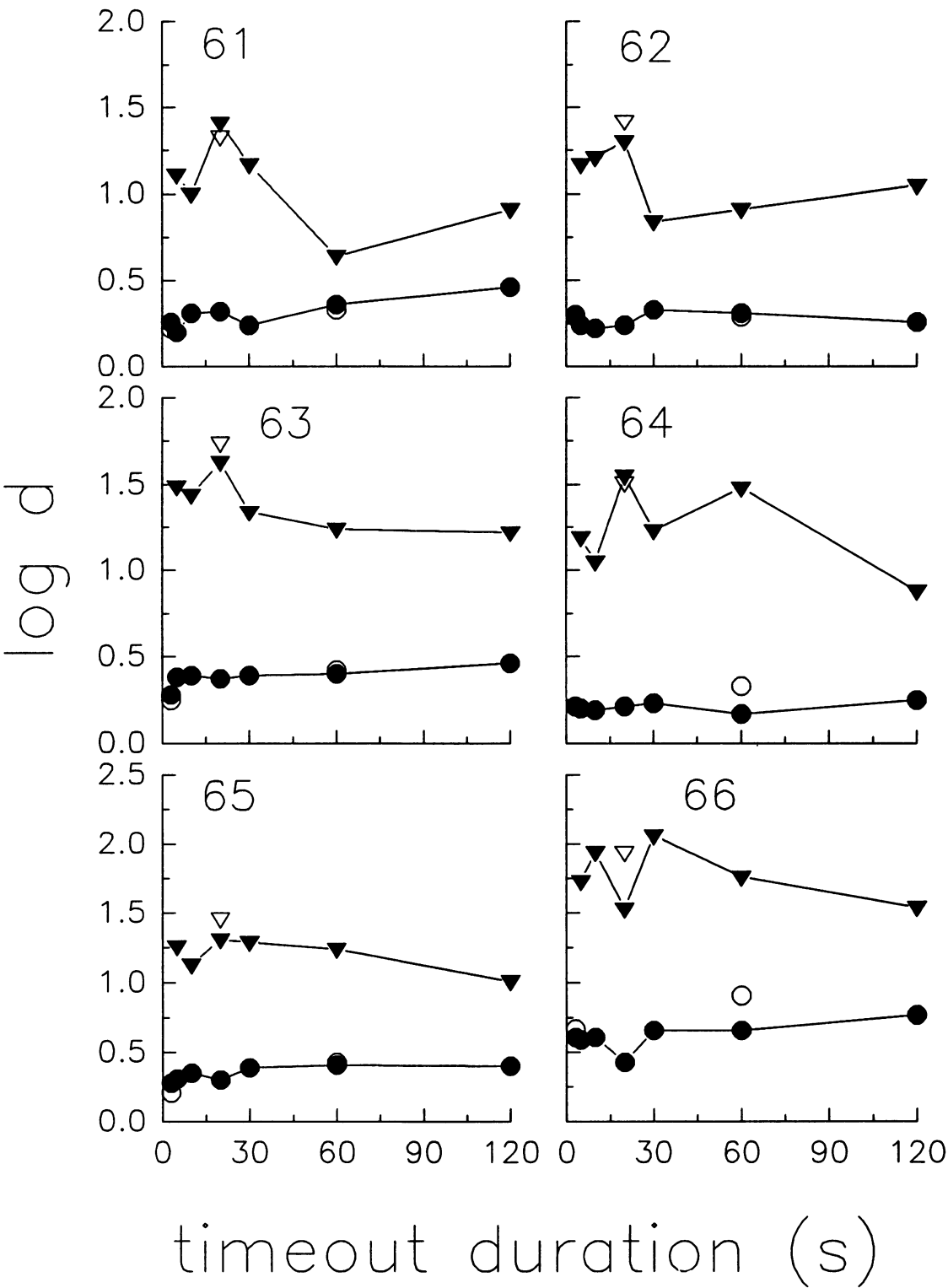


Fig. 13. Discrimination accuracy (as measured by $\log d$; Davison & Tustin, 1978) as a function of the duration of blackout arranged for false alarms in the Procedure A (circles) and Procedure B (triangles) conditions of Part 2. Unfilled symbols represent replications.

for the Procedure A (circles) and Procedure B (triangles) conditions of Part 2. These measures are plotted separately for each subject. As a result of the decreased stimulus disparity, measures of discrimination accuracy in Part 2 were, in all cases, lower than their corresponding Part 1 values. Consistent with Part 1 data, however, measures of stimulus control were again consistently higher when 3-s timeout (Procedure B) rather than 3-s reinforcement (Procedure A) was arranged for correct rejections (right/dim responses).

Possible trends across subjects in these measures as a function of the duration of timeout for false alarms were again assessed using non-parametric trend tests. Measures of $\log d$ and A' , but not proportion correct, increased monotonically with increasing timeout duration when correct rejections resulted in 3-s reinforcement (Procedure A; $z = 4.11$ and 3.62 , respectively, for $\log d$ and A' ; $p < .01$), but there were no such trends when correct rejections resulted in 3-s timeout (Procedure B; $z = 1.92$, 1.61 , and 1.46 , respectively, for $\log d$, A' , and proportion correct; $p > .01$).

Although the increase in both $\log d$ and A' in Procedure A was statistically significant, the magnitude of the increase was small in both cases: $\log d$ measures ranged from 0.32 (timeout = 3 s) to 0.43 (timeout = 120 s); A' measures ranged from 0.75 (timeout = 3 s) to 0.79 (timeout = 120 s).

Part 2: Contingency Control

Figures 14 and 15 show measures of B'' and $\log B$, respectively, as a function of the duration of timeout for false alarms in the Procedure A and Procedure B conditions of Part 2. Performance was clearly very different between the two procedures. Both measures showed that when reinforcement was arranged for correct rejections, no significant biases were evident. However, when timeout was arranged for correct rejections (so that reinforcers were only available on the left key), both measures were consistently large and indicative of a strong preference for responding on the left key (denoted by negative B'' values and positive $\log B$ values).

Measures of $\log B$ significantly decreased, and measures of B'' significantly increased, with increasing timeout duration for false alarms when correct rejections produced 3-s reinforcement (Procedure A; $z = 4.48$ and 4.84 , respectively, for $\log B$ and B'' ; $p < .01$). Spe-

cifically, response bias was negligible at the shorter timeout durations and became increasingly negative ($\log B$) or positive (B'') at the longer durations. That is, the longer the timeout on the left key, the more biased the animals became toward responding on the right key.

By contrast, when correct rejections produced 3-s timeout (Procedure B), no significant trends were seen in either measure as a function of lengthening the timeout for false alarms ($z = 1.15$ and 0.08 , respectively, for $\log B$ and B'' ; $p > .01$). However, as noted above, both measures were indicative of strong left-key preferences (mean $\log B = 0.72$; mean $B'' = -0.83$).

As was the case in Part 1, B'' and $\log B$ covaried with the log obtained reinforcer ratio in Procedure A, although this relationship was by no means perfect. For example, for Bird 66 $\log B$ decreased systematically from 0.35 to -0.34 as the duration of timeout increased, yet the log obtained reinforcer ratio varied unsystematically between 0.08 and -0.05 . At the other extreme, $\log B$ for Bird 64 varied unsystematically with timeout duration but systematically with the log obtained reinforcer ratio.

Performance on S_1 and S_2 Trials

Figure 16 shows the proportion of correct responses on S_1 (bright) and S_2 (dim) trials in Parts 1 and 2. These values were computed from group aggregate cell frequencies. Consider first the results from Part 2. In Procedure A when reinforcement was arranged for correct rejections, accuracy was approximately equal on S_1 and S_2 trials at the shortest timeout durations. However, the proportion of correct responses emitted on S_1 trials decreased with increasing timeout duration ($z = 3.62$, $p < .01$), and the proportion of correct responses made on S_2 trials increased ($z = 5.70$, $p < .01$). This indicates that response allocation on both S_1 and S_2 trials varied with timeout duration to produce the overall change in response bias toward responding on the right key (i.e., reporting S_2). In Procedure B when timeout was arranged for correct rejections, accuracy on S_1 and S_2 trials showed no change with timeout duration ($z = 0.61$ and $z = 1.15$, $p > .01$). Across all Procedure B conditions, the relative frequency of correct responses on S_1 trials was, with a single exception, either .99 or 1. "Accuracy" on S_2 trials was consistently lower and varied unsystematically with

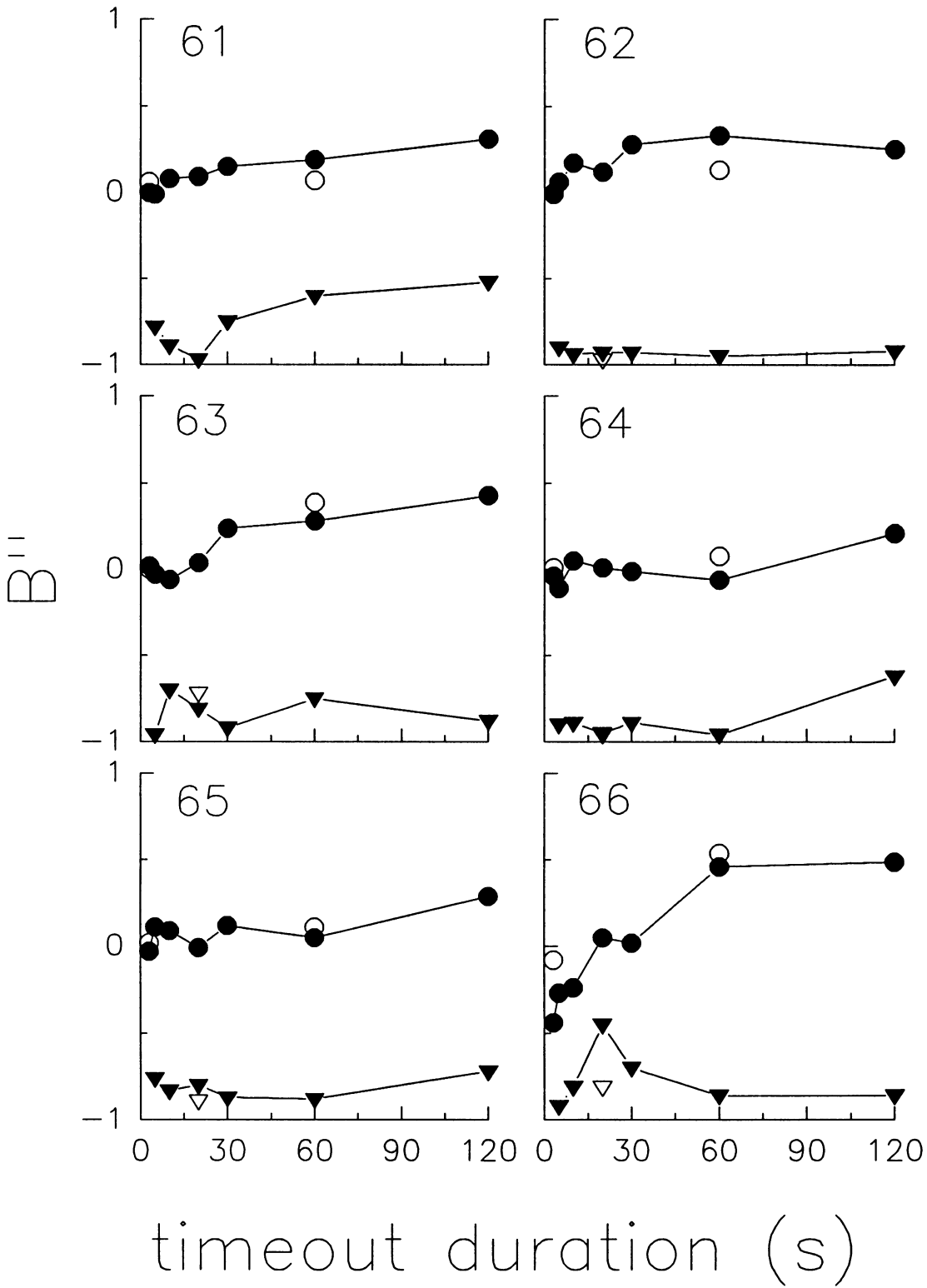


Fig. 14. Response bias (as measured by B' ; Grier, 1971) as a function of the duration of blackout arranged for false alarms in the Procedure A (circles) and Procedure B (triangles) conditions of Part 2. Unfilled symbols represent replications.

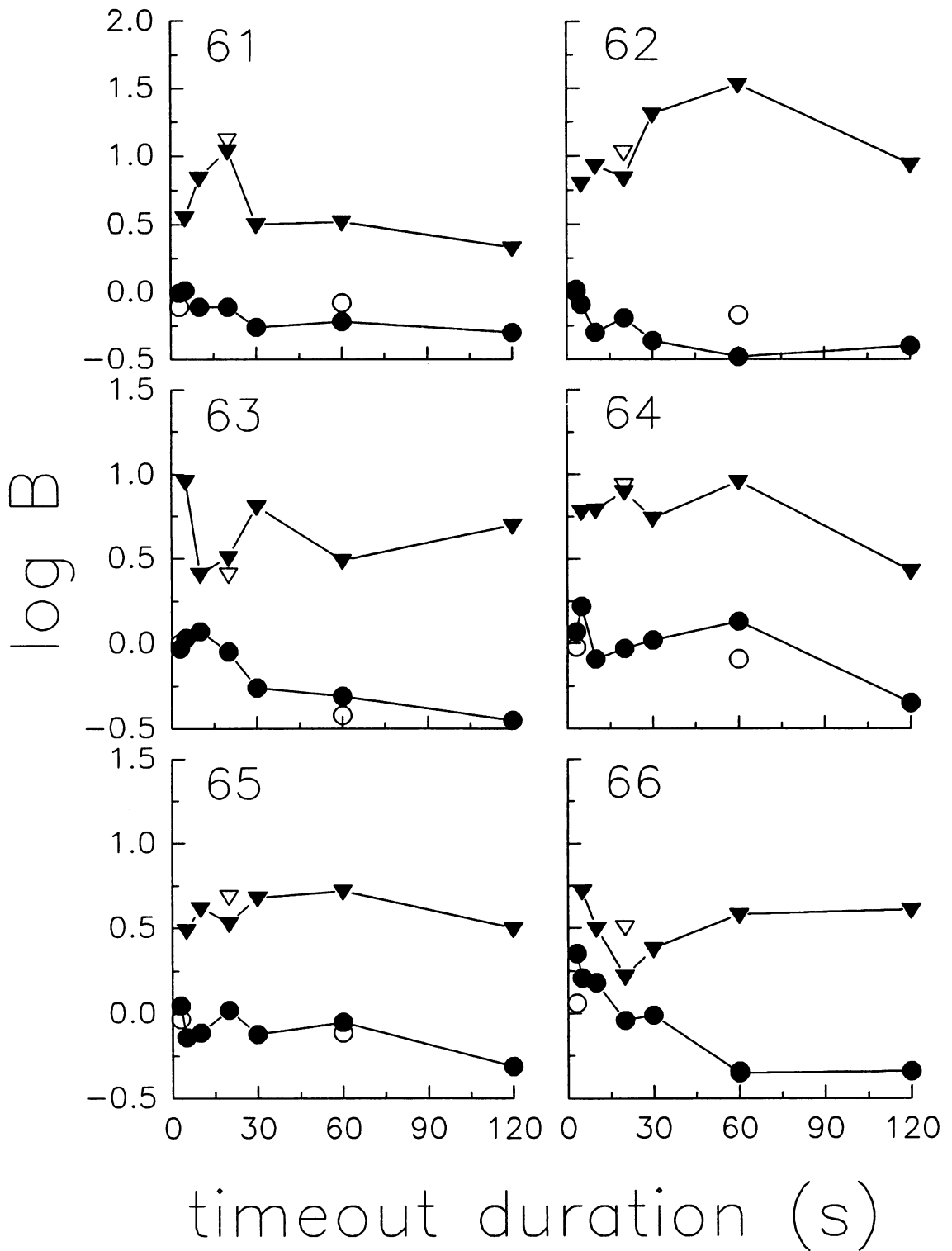


Fig. 15. Response bias (as measured by $\log B$; Davison & Tustin, 1978) as a function of the duration of blackout arranged for false alarms in the Procedure A (circles) and Procedure B (triangles) conditions of Part 2. Unfilled symbols represent replications.

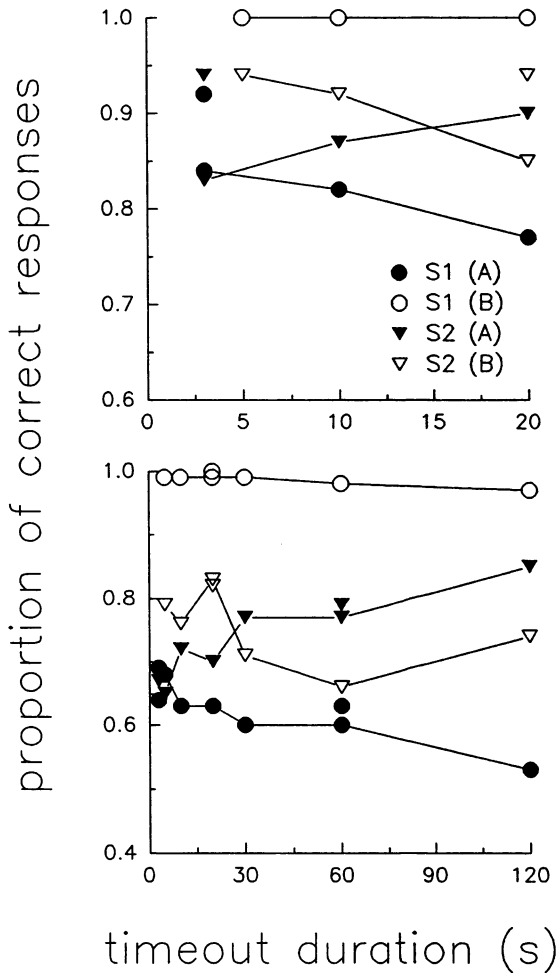


Fig. 16. The proportion of correct responses emitted on S_1 (circles) and S_2 (triangles) trials in the Procedure A (filled) and Procedure B (unfilled) conditions of Parts 1 (upper panel) and 2 (lower panel) as a function of the duration of blackout arranged for B , responses. Replications are also shown. These values were computed from the aggregate group data.

timeout duration. These effects were directionally consistent with the results of Part 1, although in Part 1 none of the trends reached statistical significance across subjects.

Comparison Between Procedure A and B Performance

For every timeout duration at which corresponding Procedure A and B conditions were arranged, accuracy was considerably higher when 3-s timeout (Procedure B), rather than 3-s reinforcement (Procedure A), was ar-

ranged for correct rejections. Similarly, response bias was numerically greater in Procedure B, indicating that performance was more biased toward reporting S_1 (a left-key response), relative to performance in Procedure A. This was true for all 6 birds in both parts of the experiment.

Arranging 3-s timeout for correct rejections (Procedure B) rather than 3-s reinforcement (Procedure A) produced greater within- and between-subject variability in measures of stimulus control and response bias (see Figures 6 to 16). This was especially so for the estimates of response bias at lower discriminability levels (Part 2). In part, this would have resulted from the very small number of right/bright responses (i.e., misses) made in most of these conditions. Once again, due to their log ratio nature, the Davison and Tustin (1978) measures (Equations 3 and 5) become somewhat unstable as cell frequencies tend to zero. Indeed, a given change in overall response allocation produced greater effects on $\log d$ and $\log B$ estimates as the minimum cell count decreased.

Finally, in most cases, all measures of accuracy and response bias computed for the replicated conditions were in reasonably close agreement with the original determinations.

DISCUSSION

When the standard detection contingencies were arranged (Procedure A; Figure 4), both accuracy and response bias varied systematically with the duration of timeout arranged for false alarms. Specifically, accuracy (as measured by A' and $\log d$) increased, albeit not very much, and responding became more biased toward the right key with increasing timeout durations. However, when the prey-detection contingencies were arranged (Procedure B; Figure 5), there was no consistent change in either accuracy or bias measures when the timeout duration for false alarms was manipulated. Furthermore, discrimination accuracy was very high, and response bias was extreme toward the left key in the prey-detection situation for all subjects. Clearly, then, measures of stimulus control were affected by manipulation of variables unrelated to the stimuli.

It is of interest to compare performance in the two detection situations arranged in the

present study with performance in comparable detection tasks. Hume and Irwin (1974) studied the performance of rats in an auditory discrimination task similar in most respects to Procedure A of the present study. Subjects were required to discriminate bursts of white noise that differed in intensity. Hits and correct rejections were reinforced with brain stimulation, whereas misses and false alarms produced periods of timeout. In their Experiment 3, the ratio of timeout durations arranged for false alarms and misses was varied over the range 1:1 to 30:1 over 13 conditions. To aid comparison, these data were reanalyzed in terms of $\log d$ (Equation 3) and $\log B$ (Equation 5). Testing for monotonic trends across subjects (Kendall, 1970), there was a statistically significant increase in accuracy ($z = 2.63$, $p < .01$) and a significant decrease (i.e., toward reporting S_2) in response bias ($z = 4.96$, $p < .01$) with increasing timeout duration ratios (false alarm/miss). In terms of trends and the magnitudes of these changes, these results are identical to those obtained in the present study.

Although there was greater within- and between-subject variability in the measures obtained in Procedure B, the results of the present study support the research that has shown the asymmetric prey-detection matrix (Figures 3 and 5) to be a stable detection situation. Kamil et al.'s (1985, Experiment 1) group data were reanalyzed in terms of Equations 3 and 5 (Davison & Tustin, 1978). Increasing the time between slide presentations (travel time) produced an orderly change in response bias ($\log B$) toward reporting the presence of a moth (from -0.21 to 0.49), but stimulus discriminability ($\log d$) was unaffected. One clear difference was that extreme "attack" biases were not found. The probable reason for this is that "attacking" slides involved the completion of a fixed-interval 30-s schedule, whereas slides could be rejected with a single response. Taking this additional biasing factor into account, the range of response biases obtained by Kamil et al. may in fact be consistent with those obtained in the present study, where the attack and reject requirements were equal.

Manipulation of Timeout Duration

When correct rejections produced 3-s reinforcement (Procedure A), response bias was closely related to the log timeout-duration ratio for false alarms and misses (median $r = -0.86$

and 0.82 for $\log B$ and B'' , respectively), but it was equally strongly related to the log obtained reinforcer ratio (median $r = 0.88$ and -0.85 for $\log B$ and B'' , respectively). On the other hand, when correct rejections produced 3-s timeout (Procedure B) and the relative distribution of reinforcers between the left and right keys was always 1.0, timeout duration had no systematic effect on response bias (or accuracy). The median correlation between response bias and the log timeout-duration ratio was -0.16 for $\log B$ and 0.04 for B'' . The systematic relationship between response bias and relative timeout duration in Procedure A strongly suggests that the changes in response bias resulted from the manipulation of timeout duration. An unsystematic relationship between these variables would have been expected if the bias changes were produced by variation in the reinforcer distribution alone. Thus, one must conclude that the timeout manipulation had a small, but consistent, effect on both accuracy and response bias. These same trends were evident in Hume and Irwin's (1974, Experiment 3) data. Here too, though, the effects of the timeout manipulation were modest compared with the 30-fold changes in relative timeout durations arranged for misses and false alarms, and compared with the large bias changes that resulted when the ratio of brain stimulation for hits and correct rejections was varied (Experiments 1 and 2).

Do the extant experimental data support the conclusion that timeout from positive reinforcement has only moderately aversive properties? Unfortunately, there is no clear answer to this question (Leitenberg, 1965).

Signal-Detection Models

Because the stimuli were unchanged across Procedures A and B within each part of the experiment, the large difference in accuracy estimates between these procedures is difficult to reconcile with the Davison and Tustin (1978) model and with traditional signal-detection theory. If Equations 1 to 3 measure the ability of the subjects to discriminate accurately between the two stimuli, these measures should have remained constant across the two procedures.

Recently, Alsop (1991) and Davison (1991) proposed a model of signal detection based on Davison and Jenkins' (1985) concurrent-schedule model. The relevant equations for

performance on S_1 and S_2 trials of the standard detection matrix (Figure 1) are

$$\frac{B_w}{B_x} = c \frac{d_s d_r R_w + R_z}{d_s R_w + d_r R_z}, \quad (6)$$

given an S_1 presentation, and

$$\frac{B_y}{B_z} = c \frac{d_r R_w + d_s R_z}{R_w + d_s d_r R_z}, \quad (7)$$

given an S_2 presentation. B_i and R_i denote the numbers of responses emitted and reinforcers obtained in cell i of the stimulus-response matrix (Figure 1), and for convenience, w = hit, x = miss, y = false alarm, and z = correct rejection. The parameter c measures any constant preference for one of the two available responses. The parameter d_s measures a subject's ability to discriminate the stimuli and is analogous to the log d measure in the Davison and Tustin (1978) model. The remaining parameter, d_r , measures the discrimination of the contingencies of reinforcement arranged for the various responses. Both d_s and d_r can take values between one (no discriminability) and infinity (perfect discriminability). Contingency discriminability (d_r) can best be viewed as the degree to which a subject is correctly able to allocate an outcome (e.g., the delivery of a food reinforcer) to the response class that produced it (e.g., a left-key response). The model assumes that the instrumental effect of a reinforcer delivered in one cell of the stimulus-response matrix generalizes to responding in each of the other cells according to the degree to which the two stimulus-response-outcome complexes may be confused.

Extending this model to include the interaction of both reinforcement (hits and correct rejections) and punishment (misses and false alarms) requires an additional parameter, d_p , to measure the discriminability of the response-punishment contingencies. The full equations are

$$\frac{B_w}{B_x} = c \frac{d_s d_r R_w - \alpha d_s P_x - \beta d_p P_y + R_z}{d_s R_w - \alpha d_s d_p P_x - \beta P_y + d_r R_z} \quad (8)$$

and

$$\frac{B_y}{B_z} = c \frac{d_r R_w - \alpha P_x - \beta d_s d_p P_y + d_s R_z}{R_w - \alpha d_p P_x - \beta d_s P_y + d_s d_r R_z}, \quad (9)$$

where P_i denotes the obtained frequency of punishment in cell i , and α and β are scaling factors relating reinforcement and punishment

parameters on a single dimension. Separate scalars have been included to deal with the case in which the punishers delivered in the x and y cells differ in duration, intensity, or the like. In the present study, $\beta \geq \alpha$. In writing Equations 8 and 9, it is assumed that the effects of contingent punishment on a particular behavioral activity subtract from the effects of contingent reinforcement. This assumption is essentially the basis of the subtractive model of punishment proposed by de Villiers (1980, 1982), Farley (1980), and Farley and Fantino (1978) to account for the effects of electric shock. In the case of timeout from positive reinforcement, this assumption may be questionable, because there is evidence (e.g., Dunn, 1990) that a subtractive model may not account well for some timeout effects.

In the prey-detection matrix (Figure 5), the contingencies arranged for right-key responses (B_x and B_z) are identical. Thus, Equations 10 and 11 describe performance on S_1 and S_2 trials, respectively:

$$\frac{B_w}{B_x} = c \frac{d_s d_r R_w - \alpha(d_s P_x + P_z) - \beta d_p P_y}{d_s R_w - \alpha d_p(d_s P_x + P_z) - \beta P_y} \quad (10)$$

and

$$\frac{B_y}{B_z} = c \frac{d_r R_w - \alpha(P_x + d_s P_z) - \beta d_s d_p P_y}{R_w - \alpha d_p(P_x + d_s P_z) - \beta d_s P_y}. \quad (11)$$

Because the ratio of reinforcers obtained for left- and right-key responses was not varied systematically in the present study, an analysis in terms of the Alsop (1991) and Davison (1991) model is not possible. However, several comments can be made regarding this model and its predictions.

First, arranging qualitatively or quantitatively different punishers for misses and false alarms should affect the discriminability of the response-punisher contingencies. For example, all else being equal, d_p should be greater if misses and false alarms produce timeout and electric shock, respectively, than if both produce timeout. Similarly, in the present study, d_p and β should be proportional to the duration of timeout contingent upon false alarms, and therefore should vary across conditions within each procedure.

Second, accuracy increased (albeit slightly) as a function of the duration of timeout for false alarms in Procedure A of the present

study. This result is consistent with the model outlined above. The appropriate equations to describe performance in Procedure A (Figure 4) are Equations 8 and 9. Assuming that d_p varies with the duration of timeout arranged for false alarms, the model predicts the obtained increase in accuracy.

Finally, as α and β tend to zero, the effect on behavior of a single delivered punisher diminishes. The modest effects of the timeout manipulation on response bias in both procedures imply that α and $\beta < 1$.

The "Differential-Outcomes Effect"

The large and consistent difference between accuracy obtained in Procedure A, in which correct rejections were reinforced, and in Procedure B, in which correct rejections produced timeout, may be an example of the so-called "differential-outcomes effect" (Trapold, 1970). Accuracy in a conditional discrimination task is greater when the two correct responses produce different outcomes than when they produce a common outcome. This effect has been demonstrated when the outcomes for correct responses differ in probability of reinforcement (DeLong & Wasserman, 1981), reinforcer quality (Trapold, 1970), reinforcer magnitude (Carlson & Wielkiewicz, 1976), and delay of reinforcement (Carlson & Wielkiewicz, 1972). Most relevant to the present study, Peterson, Wheeler, and Trapold (1980) have shown that accuracy is enhanced even when the differential outcomes are reinforcement and nonreinforcement. In the present study, enhanced accuracy has been demonstrated within the same group of subjects, rather than between groups. Furthermore, the effect was shown to be reversible for all subjects (Figures 11, 12, and 13).

The differential-outcomes effect fits comfortably within the conceptual framework of the Alsop (1991) and Davison (1991) d_s - d_r model. In a discrete-trials conditional discrimination task, the response alternative defined as "correct" depends on the stimulus presented on that trial. Clearly, the ability to respond accurately is a function of the disparity of the sample stimuli. As these stimuli are made more similar, accuracy must decrease (e.g., White, 1985). Similarly, accuracy declines as the responses (e.g., Eckerman, 1970) or the outcomes of the responses (e.g., Davison & McCarthy, 1980) are made more similar. At the

limit, if the responses or the set of possible outcomes are indiscriminable, accuracy must fall to chance levels. Conversely, as the responses or their outcomes become more differentiated, accuracy should increase. In the Alsop and Davison model, the relation between behavior and stimulus disparity is measured by the parameter d_s , and the relation between behavior and response or outcome disparity is measured by d_r . Viewing the sample stimulus, the response, and the outcome of the response as a complex behavioral unit (or as Nevin, Jenkins, Whittaker, & Yarensky, 1982, have elegantly suggested, a *discriminated operant*), then, the two "correct" discriminated operants should be more discriminable under differential-outcome conditions than under common-outcome conditions. Assuming all other aspects of the detection situation to be constant (and in particular that $d_s > 1$), reinforcing all responses equally (the "reinforcement-for-errors" procedure, e.g., Davison & McCarthy, 1980; Nevin et al., 1982; Nevin, Olson, Mandell, & Yarensky, 1975) should result in a minimal d_r value. Delivering reinforcers in the w and z cells only (the standard procedure) should produce an intermediate d_r value. Finally, when reinforcers are delivered in only one cell (the differential-outcomes procedure), d_r should be maximal. Accuracy increases across these three procedures as a function of the ease with which the discriminated operants can be distinguished.

To summarize, the Alsop (1991) and Davison (1991) model provides a conceptual framework that clarifies the relationship between the differential-outcomes and reinforcement-for-errors procedures and more conventional signal-detection procedures.

Conclusion

The signal-detection analogy (e.g., Getty et al., 1987; Staddon, 1983) represents a promising approach to the study of prey detection. The experimental procedures that have been developed to investigate signal-detection performance in animals (see Davison & McCarthy, 1988) seem ideally suited for this application.

In the present study, increasing the duration of timeout arranged for false alarms had a consistent, but relatively small, effect on performance in the standard detection task (Procedure A; Figure 4). In contrast, the effects of

this manipulation on performance in the prey-detection task (Procedure B; Figure 5) were inconsistent, with considerable within- and between-subject variability. Although the asymmetric prey-detection matrix represents a stable detection situation, the performance that it maintains clearly differs from that maintained by the standard symmetric matrix. Specifically, performance in the prey-detection situation was characterized by greater measured discrimination accuracy, as well as by a large bias toward the response associated with reinforcement.

Stating these results in ecological terms, the effects of increasing the penalty for incorrectly attacking nonprey items on subjects' biases toward attacking or rejecting potential prey items and on their accuracy in discriminating prey from nonprey were consistent when correct rejections were reinforced, but were inconsistent when correct rejections were not reinforced.

It was argued that differential-outcome procedures, such as the prey-detection procedure arranged in the present study, and reinforcement-for-errors procedures can be united with more standard detection procedures in a single framework by considering the similarity of the outcomes arranged for the stimulus-response classes. The signal-detection model proposed by Alsop (1991) and Davison (1991) includes a parameter that measures the discriminability of these response-outcome contingencies. This model successfully predicts the differences in discrimination accuracy found between these procedures.

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Received May 22, 1992

Final acceptance March 9, 1993

APPENDIX

Individual data summed over the final seven sessions of each experimental condition. These data are the number of left- and right-key responses following S₁ (bright) and S₂ (dim) presentations on the center key.

Condition	Left/ bright	Right/ bright	Left/ dim	Right/ dim
Bird 61				
1	150	67	69	130
2	146	65	51	134
3	129	89	38	151
4	280	1	86	218
5	280	1	19	258
6	280	1	19	251
7	280	0	12	276
8	131	16	16	149
9	136	45	37	144
10	130	72	81	150
11	280	1	81	187
12	280	6	61	221
13	280	4	113	164
14	280	0	102	166
15	133	81	55	147
16	139	85	91	141
17	131	82	57	149
18	119	86	43	161
19	114	119	53	166
20	136	93	25	144
21	189	11	38	146
22	280	6	52	246
23	259	18	126	164
24	136	77	56	144
25	126	97	72	154
Bird 62				
1	139	16	21	141
2	133	30	13	147
3	126	44	14	154
4	280	0	45	241
5	280	0	33	266
6	280	0	24	246
7	280	0	16	296
8	132	2	1	148
9	135	24	18	145
10	140	67	73	140
11	280	2	73	210
12	280	3	86	204
13	280	2	101	194
14	280	1	74	183
15	119	107	59	161
16	128	92	71	152
17	103	123	53	177
18	90	131	31	190
19	109	115	35	171
20	109	151	37	171
21	196	2	90	118
22	280	2	253	86
23	273	1	237	57
24	127	98	53	153
25	139	70	72	141
Bird 63				
1	145	15	20	135
2	131	44	18	149

APPENDIX (Continued)

Condition	Left/ bright	Right/ bright	Left/ dim	Right/ dim
3	123	35	10	157
4	280	2	53	226
5	280	2	23	232
6	280	1	22	212
7	280	0	38	267
8	145	26	12	135
9	130	31	31	150
10	131	74	72	149
11	280	2	20	265
12	280	1	69	233
13	280	4	24	256
14	280	2	12	253
15	137	65	55	143
16	146	57	60	134
17	150	53	62	130
18	113	91	33	167
19	114	86	37	166
20	120	118	20	160
21	167	2	39	130
22	280	2	56	190
23	264	5	40	226
24	115	114	24	165
25	145	82	76	135
Bird 64				
1	134	26	18	146
2	137	12	15	143
3	146	30	16	134
4	280	3	36	249
5	280	1	15	298
6	280	0	7	236
7	280	0	16	249
8	143	17	16	137
9	138	31	22	142
10	149	78	93	131
11	280	0	54	240
12	280	3	78	202
13	280	4	98	179
14	280	0	57	209
15	145	96	79	135
16	164	63	121	116
17	127	102	80	153
18	167	82	103	113
19	144	81	82	136
20	117	149	41	163
21	183	9	51	144
22	280	3	69	209
23	276	1	62	203
24	135	79	55	145
25	136	89	85	144
Bird 65				
1	136	33	24	144
2	137	25	19	143
3	145	25	20	135
4	280	0	30	254
5	280	0	34	292
6	280	0	12	262
7	280	0	13	242
8	136	7	8	144
9	138	19	16	142
10	152	72	76	128

APPENDIX (*Continued*)

Condition	Left/ bright	Right/ bright	Left/ dim	Right/ dim
11	280	4	41	245
12	280	5	44	258
13	280	5	67	216
14	280	2	40	238
15	140	67	72	140
16	123	84	55	157
17	139	79	49	141
18	150	66	45	130
19	125	68	48	155
20	125	102	30	155
21	194	6	45	143
22	280	3	51	211
23	270	3	60	199
24	129	61	44	151
25	133	88	84	147
Bird 66				
1	142	8	13	138
2	146	5	12	134
3	133	13	4	147
4	280	0	13	270
5	280	0	11	275
6	280	0	7	278
7	280	0	10	255
8	128	2	3	152
9	151	11	20	129
10	163	18	64	117
11	280	5	13	262
12	280	1	23	239
13	280	0	10	275
14	280	1	10	269
15	142	58	46	138
16	144	23	56	136
17	148	24	48	132
18	127	63	15	153
19	138	31	30	142
20	139	52	11	141
21	142	1	15	126
22	280	1	5	239
23	222	0	14	213
24	138	37	8	142
25	144	27	33	136